

# The re-discovered *Maculinea rebeli* (Hirschke, 1904): Host ant usage, parasitoid and initial food plant around the type locality with taxonomical aspects (Lepidoptera, Lycaenidae)

András Tartally<sup>1</sup>, Anton Koschuh<sup>2,†</sup>, Zoltán Varga<sup>1</sup>

**1** Department of Evolutionary Zoology and Human Biology, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary **2** Steyrergasse 72/8 A-8010 Graz, Austria

Corresponding author: András Tartally (tartally.andras@science.unideb.hu)

---

Academic editor: C. Peña | Received 24 January 2014 | Accepted 14 April 2014 | Published 29 April 2014

---

**Citation:** Tartally A, Koschuh A, Varga Z (2014) The re-discovered *Maculinea rebeli* (Hirschke, 1904): Host ant usage, parasitoid and initial food plant around the type locality with taxonomical aspects (Lepidoptera, Lycaenidae). ZooKeys 406: 25–40. doi: 10.3897/zookeys.406.7124

---

## Abstract

The taxonomy of the myrmecophilous *Maculineaalcon* group (Lepidoptera: Lycaenidae) is highly debated. The host-plant and host-ant usage of these butterflies have conventionally been important in their identification. *Maculinea 'rebeli'* has generally been considered to be the xerophilous form of *Ma.alcon* (*Ma.alcon X* hereafter) with *Gentiana cruciata* as initial food plant. However, the type locality and all other known sites of *Ma. rebeli* are found above the coniferous zone, and are well separated from the lower regions where *Ma.alcon X* sites are found. Furthermore, no food plant and host ant data for the nominotypic *Ma. rebeli* have yet been published. Our aim was therefore to identify the host ant(s) of *Ma. rebeli* around the type locality and compare this with the host ant usage of nearby *Ma.alcon X*. Nests of *Myrmica* spp. (Hymenoptera: Formicidae) close to the host plants were opened on one *Ma.alcon X* (host plant: *Gentiana cruciata*) and two *Ma. rebeli* (host plant: *Gentianella rhaetica*, first record, confirmed by oviposition and emerging larvae) sites just before the flying period, to find prepupal larvae and pupae. Three *Myrmica* species (*My.lobulicornis*, *My.ruginodis*, *My.sulcinodis*) were found on the two *Ma. rebeli* sites, which parasitized exclusively *My. sulcinodis* (22 individuals in 7 nests). On the *Ma.alcon X* site *Myrmica sabuleti* and *My. lonae* were found, with *My. sabuleti* the exclusive host (51 individuals in 10 nests). *Ichneumon* cf. *eumerus* parasitized both butterflies. The results highlight the differentiation of *Maculinea rebeli* from *Ma.alcon X*, from both conservation biological and ecological points of view. Thus, it should be concluded that *Ma. rebeli* does not simply represent an individual form of *Ma.alcon* but it can be considered as at

---

† 1970–2013

least an ecological form adapted to high mountain conditions both in its initial food plant and host ant species. In addition, it should be emphasized that *Ma. alcon* X (= *Ma. rebeli* auct. nec Hirschke) cannot be synonymised with *Ma. rebeli* (Hirschke, 1904).

### Keywords

Styrian Alps, nominotypic *Maculinea rebeli*, *Myrmica sulcinodis*, *My. sabuleti*, *Gentianella rhaetica*, *Ichneumon* cf. *eumerus*

### Introduction

Although *Maculinea* van Eecke, 1915 (Lepidoptera, Lycaenidae) has been synonymised with *Phengaris* Doherty, 1890 (see: Fric et al. 2007, Pech et al. 2007, Kudrna and Fric 2013) we continue to use the well-established generic name here, since (i) the case is still undecided by the International Commission on Zoological Nomenclature (ICZN 2012) and strong arguments for the precedence of *Maculinea* over *Phengaris* have been made (Balletto et al. 2010, and Comments on this Case); and (ii) Ugelvig et al. (2011) have shown that *Maculinea* represents a monophyletic sub-clade and we agree with their conclusion: “*We recommend that the nomenclatural debate is delayed until irrefutable evidence is provided*”.

*Maculinea* (abbreviated as “*Ma.*” below) butterflies are endangered species (Mun˘guira and Martın 1999, Maes et al. 2004, Settele et al. 2005) and their larvae are social parasites of *Myrmica* Latreille, 1804 (Hymenoptera: Formicidae; abbreviated as “*My.*” below) ant colonies (Thomas et al. 1989). Larvae of *Maculinea alcon* ([Denis & Schiffermuller], 1775) initially feed on the seeds of gentian plants for about a month and are later taken in and raised by *Myrmica* colonies (Thomas et al. 1989). They have a “cuckoo” strategy, in which they mimic the odour (Thomas and Settele 2004, Nash et al. 2008, Akino et al. 1999) and sound (Barbero et al. 2009) of the host ant species, and are therefore fed like an ant larva (Thomas and Elmes 1998), although they also sometimes prey directly on the ant brood (Tartally 2004). The caterpillars develop within the host ant nest during the autumn, winter and spring, and will then either pupate there, or continue development for an additional year (Schonrogge et al. 2000, Witek et al. 2006).

There are regional and local differences between the host ant usage of different populations (e.g. Elmes et al. 1994, Als et al. 2002, Hottinger et al. 2003, Steiner et al. 2003, Sielezniew and Stankiewicz 2004, Stankiewicz et al. 2005, Tartally et al. 2008, Witek et al. 2008, Tartally et al. 2013). Knowledge of the local host ant species is vital to understand the biogeography, conservation and evolutionary biology of *Maculinea* spp. (Settele et al. 2005, Settele and Kuhn 2009), and may also have some taxonomic implications. Furthermore, the host ant and host plant usage of *Ma. alcon* has been thought to be important for taxonomic separation (Thomas et al. 1989) of the hygrophilous (*Ma. alcon* H’ below) and the xerophilous (*Ma. alcon* X’) form of *Ma. alcon*, although recent studies have been unable to show any consistent genetic separation between these two butterflies (Als et al. 2004, Bereczki et al. 2005, Ugelvig et al. 2011).

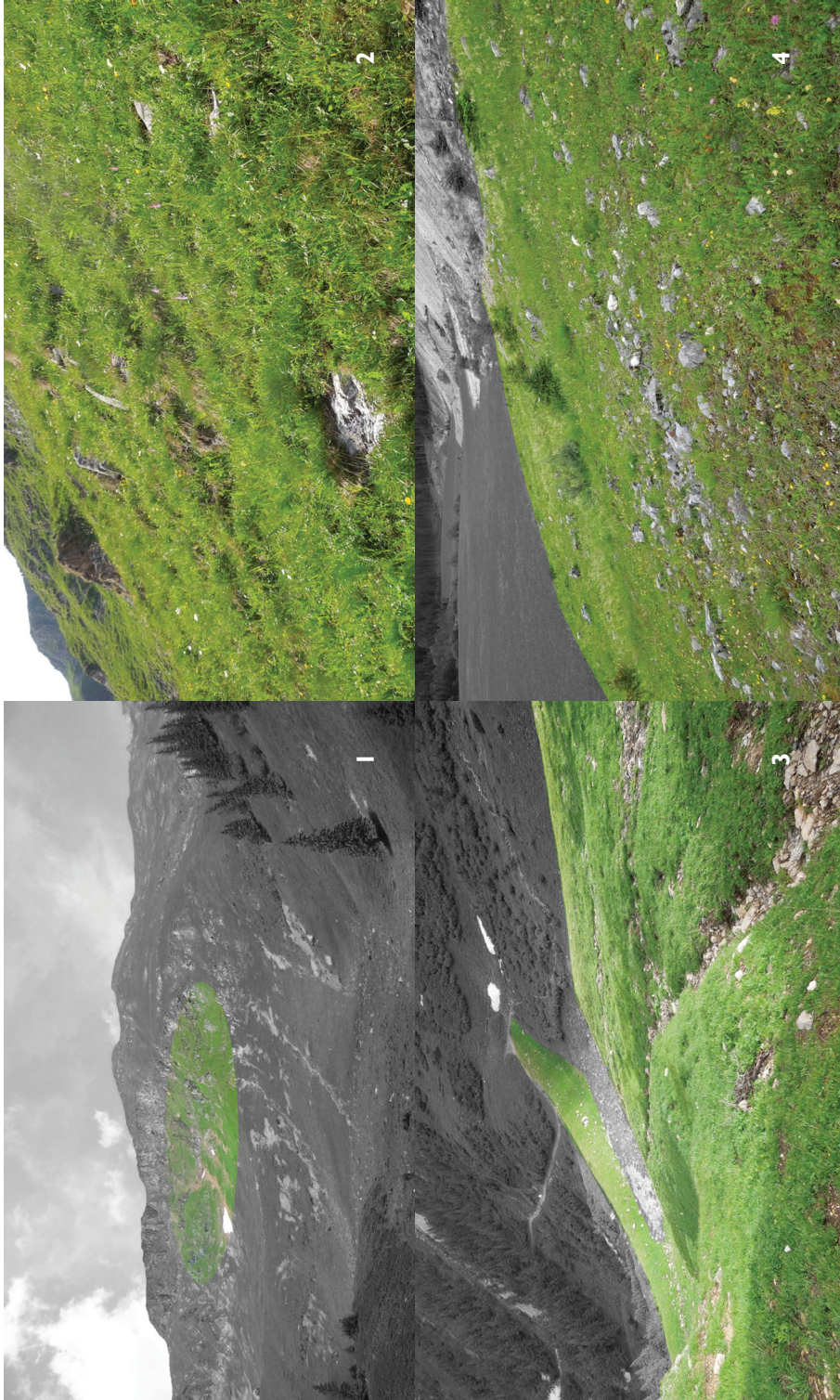
Despite this, *Ma. alcon X* is still generally (and erroneously, see Kudrna and Fric 2013) referred to as '*Ma. rebeli* (Hirschke, 1904)' (e.g. Elmes et al. 1998, Steiner et al. 2003, Stankiewicz et al. 2005, Tartally et al. 2008). Some Balkan, Caucasian and Central Asian mountainous populations of *Ma. alcon* have also been referred to as *Ma. 'rebeli'* (Kolev 2002, Savela 2014, Tuzov 2000).

However, a recent paper (Habeler 2008) called our attention to the fact that *Ma. alcon X* (= *Ma. rebeli* auctorum nec Hirschke, 1904) is not likely synonymous with *Ma. rebeli* described by Hirschke (1905) from the type locality, based on external morphological features and the different habitat types in which they occur. It has now been demonstrated that *Ma. rebeli* auct. does not represent a distinct species, but rather the xerophilous form of *Ma. alcon* (*Ma. alcon X*). It feeds initially typically on *G. cruciata* (Bereczki et al. 2005, Pecsénye et al. 2007, Sielezniew et al. 2012) then using mainly *Myrmica schencki* Viereck, 1903, *My. sabuleti* Meinert, 1861 and some other available *Myrmica* species (e.g. Elmes et al. 1998, Meyer-Hozak 2000, Steiner et al. 2003, Stankiewicz et al. 2005, Tartally et al. 2008). However, following the paper of Habeler (2008), we realised that no reliable host ant and initial food plant data have been published for the nominotypic *Ma. rebeli* (called simply *Ma. rebeli* hereafter).

The main reason for our study is that the type locality and the other suggested sites of *Ma. rebeli* are above the coniferous zone and well-separated by spruce forests (see Figure 7 in Habeler 2008) from the lower regions where *Ma. alcon X* occurs in grasslands (mostly extensive pastures) with *G. cruciata*. Furthermore, from our personal observations (see Materials and Methods), *Ma. rebeli* uses *Gentianella rhaetica* (A. Kern. & Jos. Kern.) Á. Löve & D. Löve rather than *G. cruciata* at higher altitudes, as the latter plant is not available in that zone (see the questions about host plant usage of Kudrna and Fric 2013). Similarly, we reasoned that the available *Myrmica* species are likely to be different for *Ma. rebeli* and *Ma. alcon X* within the same region because of changes in available niches with increasing altitude (Elmes et al. 1998, Glaser 2006). It is therefore important to know the host ant use and specificity of *Ma. rebeli* and *Ma. alcon X* around the type locality of *Ma. rebeli* to help in answering the question of whether these two butterflies should be treated as the same or different forms or species.

## Methods

Three sites within the Hochschwab area (Styrian Alps, Austria; Figs 1–4) were visited between the 22<sup>nd</sup> and 24<sup>th</sup> June 2012 (just before the flying period). Two *Ma. rebeli* habitats above the coniferous zone were investigated, one at Zeiritz (47.486N, 14.723E, ca 1750 m a.s.l.) and another at Präbichl (47.512N, 14.938E, ca 1600 m a.s.l.). Both sites are sparsely covered by calcareous alpine *Sesleria varia* (Jacq.) Wettst.-*Carex sempervirens* Vill. grassland (Seslerio-Semperviretum) vegetation on stony and sunny slopes, with bare limestone rocks (Figs 1–3, compare with Figs 8–10 in Habeler 2008). We regularly found eggs on *Gentianella rhaetica* (Fig. 5; det. K. Zernig,



**Figure 1–4.** 1–2 *Maculinea rebeli* site at Zeiritz above the coniferous zone (1750 m) 3 *Ma. rebeli* site at Pr abichl above the coniferous zone (1600 m) 4 *Ma. alcon* X site at Sankt Ilgen within the coniferous zone (photo: AK).

Universalmuseum Joanneum; it belongs to the *Gentianella germanica* agg.: Greimler et al. 2011) on both sites, and caterpillars readily developed on and emerged from this plant (AK and AT, pers. observ.). The third site is a calcareous grazed meadow (Fig. 4) within the coniferous zone (Sankt Ilgen: 47.562N, 15.153E, ca 810 m a.s.l.) where *Ma.alcon X* uses *Gentiana cruciata* as initial host plant (an adjacent similar site for *Ma.alcon X* has already been described by Bereczki et al. 2005 and Pecsénye et al. 2007).

The host ant specificity of the *Ma.alcon X* population at Sankt Ilgen was checked by searching for *Myrmica* spp. nests within 2 m of *G. cruciata* plants (see details: Tartally et al. 2008). However, this method was not possible in the case of the two *Ma. rebeli* sites (at Prächichl and Zeiritz) as *Gentianella rhaetica* plants are rather small before the flying period of *Ma. rebeli*, and were only rarely visible. We instead worked within patches where *G. rhaetica* plants were found in the previous year (although it should be noted that we were often not sure of the actual presence of plants in 2012, as *G. rhaetica* is biannual). When a *Myrmica* nest was found, it was opened as carefully as possible to search for *Maculinea* larvae and pupae. Five to ten workers were collected from each ant nest and preserved in 75% ethanol for identification in the laboratory (following keys in Seifert 1988, Radchenko and Elmes 2010, Czechowski et al. 2012).

Host ant specificity was calculated based on the number of fully grown butterfly larvae, pupae and exuvia found (i.e., not including small larvae: see results) in two ways (see details: Tartally et al. 2008): p1 is the 2-tailed probability from a Fisher exact test of heterogeneity in infection of host ant nests (as implemented at <http://www.quantitativeskills.com/sisa/>), and p2 is the probability from a randomization test of ant nests between species (using the program MacSamp; Nash 2014). We should emphasize that our data on the host ant specificity of *Ma. rebeli* and *Ma.alcon X* should be compared cautiously, as our certainty of the presence of host plants differed for *Ma. rebeli* and *Ma.alcon X* (see above). Furthermore, excavating complete nests of *Myrmica* spp. was relatively easy in the deep humus of the *Ma.alcon X* site, but was much more difficult in the rocky *Ma. rebeli* sites.

## Results

Altogether 53 *Myrmica* nests were found on the three sites (Table 1), consisting of 52 nests of five *Myrmica* species and one empty (presumably recently vacated) but *Maculinea*-infested nest which was similar in appearance to nearby *My. sabuleti* nests. Only nests of *My. sabuleti* and of the closely related (Radchenko and Elmes 2010) *My. lonae* Finzi, 1926 were found at the *Ma.alcon X* site (Sankt Ilgen), whereas the *Myrmica* composition of the two *Ma. rebeli* sites was totally different from this: *My. ruginodis* Nylander, 1846 and *My. sulcinodis* Nylander, 1846 were found at both sites, plus *My. lobulicornis* Nylander, 1857 at Prächichl.

Nine nests of *My. sulcinodis* were infested with 33 *Ma. rebeli* larvae, pupae and exuvia at Prächichl and Zeiritz in total, of which 11 caterpillars were so small as to



**Figure 5–7.** 5 *Ma. rebeli* eggs on *Gentianella rhaetica* at Prábichl 6 *Ma. rebeli* pupae under a stone in a *Myrmica lobulicornis* nest at Zeitzitz 7 *Ma. alcon* X pupae and a small larva found in *Myrmica sabuleti* nest at Sankt Ilgen, arrows sign infections with *Ichneumon* cf. *enumerus* (photo: AK).

**Table 1.** The recorded *Myrmica* spp. nests and host ant usage of *Maculinea rebeli* (at Präbichl and Zeiritz), *Ma. alcon* X (at Sankt Ilgen) and *Ichneumon* cf. *emerus* according to the number of large larvae, pupae and exuvia (= "grown *Maculinea*") and according to these together with the small larvae (= "*Maculinea* in total"). Two measures of host specificity are given: P1 is the 2-tailed probability from the Fisher exact test of heterogeneity in infection of host ant nests and P2 is the probability from a randomization test of ant nests between species (see Materials and Methods).

Site	No. <i>Myrmica</i> nests	Nests Infested with grown <i>Maculinea</i>	No. grown <i>Maculinea</i> (range, P1, P2)	Nests Infested with <i>Maculinea</i> in total	No. <i>Maculinea</i> in total (range, P1, P2)	No. nests Parasitized with <i>I. cf. emerus</i>	No. <i>I. cf. emerus</i> (range, P1, P2)
Präbichl ( <i>Ma. rebeli</i> )	lobulicornis 3						
	ruginodis 1						
	sulcinodis 13	4	15 (2-7, 0.64, 0.62)	6	25 (2-7, 0.34, 0.39)	2	8 (2-6, 0.43, 0.86)
Zeiritz ( <i>Ma. rebeli</i> )	ruginodis 8						
	sulcinodis 13	3	7 (2-4, 0.26, 0.35)	3	8 (1-3, 0.26, 0.25)	1	1 (1-1, 1.00, 1.00)
Sankt Ilgen ( <i>Ma. alcon</i> X)	lonae 1						
	sabuleti 13	10	51 (1-11, 0.26, 0.50)	10	53 (1-11, 0.26, 0.50)	9	28 (1-8, 0.36, 0.64)
	empty nest 1	1	9	1	9	1	8

be two-year developing larva after their first winter. There were 15 pupae in total on these two sites, nine of which (60%) proved to be infected with *Ichneumon* cf. *eumerus* Wesmael, 1857.

Ten nests of *My. sabuleti* were infested at Sankt Ilgen with 53 *Ma. alcon* X larvae, pupae and exuvia, but only two caterpillars were so small as to be two-year developing larvae. There were nine “orphaned” *Ma. alcon* X pupae in the empty nest, which were dirty and showed visible signs of external mould. There were 36 pupae in total, 28 of which (77.8%) were infected with *Ichneumon* cf. *eumerus*.

## Discussion

Based on the character of the habitat, the figures published by Habeler (2008) and photographs of *Ma. rebeli* imagos taken by AK (Figs 8–9), we are confident that we have re-discovered two populations that correspond to the description of Hirschke (1905). Our data confirm that *Ma. rebeli* is (at least) an ecological form found at high altitudes, and with host ant and initial food plant distinct from the adjacent populations of *Ma. alcon* X (*Ma. rebeli* auct. nec Hirschke). It is unlikely to be a mere individual form characterised “by the presence of a band of whitish or silver-greyish spots in the blue ground colour in the submarginal band adjacent to the marginal black line on the upper side of wings, particularly well pronounced on the hind wings and especially in the ♀” (see Kudrna and Fric 2013 page 117, which is a misinterpretation of the original German text of Hirschke (1905): 109–110: „Am Innenwinkel der Vorderfl gel zeigt sich in Zelle 2 und 3 eine auffallende Aufhellung, welche sich auf die Hinterfl gel fortsetzt und gegen den Innenwinkel derselben sogar die Form einer Antemarginalbinde gewinnt.”). Furthermore, the specimens figured by Habeler (2008) also clearly show this character of *Ma. rebeli* but they are simply darker than the type series of Hirschke (1905) due to the circumstance that they were captured quite recently (1978–2005) while the type series was collected in 1904.

To avoid further confusion, we argue that the true *Ma. rebeli* occurs in the Hochschwab area above the coniferous zone (between c.a. 1500 and 2000 m) on slightly covered stony and sunny slopes with uncovered chalk rocks, where *G. rhaetica* is the only recorded initial host plant, and *My. sulcinodis* is the only recorded host ant species so far. We still need to confirm the observation of Habeler (2008) that these high altitude habitats are usually small, fragmented, and often located on steep and inaccessible (see Fig. 1) slopes, but it does seem that these populations have remained unknown to (or neglected by) most authors (see Kudrna and Fric 2013).

As far as we know, our observations are the first data on the host ant specificity of *Ma. rebeli* around the type locality, and hence, we maintain, of the host ant specificity of *Ma. rebeli*. Earlier data about the host ant specificity of *Ma. ‘rebeli’* (e.g. Elmes et al. 1998, Meyer-Hozak 2000, Steiner et al. 2003, Stankiewicz et al. 2005, Tartally et al. 2008) should instead be considered as data about the host ant specificity of *Ma. alcon* X (see Introduction and Habeler 2008). While *Ma. rebeli* was found exclusively





Figure 8–9. 8 *Ma. alcon* X (Hochschwab area) 9 *Ma. rebeli* (Hochschwab area) (photo: AK).

in *Ma. sulcinodis* nests at Zeiritz and Pr bichl, the works just cited mention *Ma.alcon X* generally from nests of *Myrmica schencki* or *My. sabuleti* and from some other locally available *Myrmica* species (*My. lonae*; *My. scabrinodis* Nylander, 1846; *My. specioides* Bondroit, 1918; *My. rugulosa* Nylander, 1849; and *My. ruginodis*). However, we cannot rule out the discovery of other host ants of *Ma. rebeli* in the Hochschwab region, following more intensive work. H.C. Wagner (see Kudrna and Fric 2013) also found *Myrmica sulcinodis*, *My. ruginodis* and *My. lobulicornis* as available *Myrmica* species on *Ma. rebeli* sites, plus one nest of *My. scabrinodis*, and also suggested *My. lobicornis* Nylander, 1846 as a potentially available but unrecorded species. Jutzeler (1989) has previously recorded *My. sulcinodis* interacting with a full-grown larva of *Ma. 'rebeli'* in the Swiss alps, although it was unclear whether this was a host nest or opportunistic predation (see also: Kudrna and Fric 2013). Although he did not record the altitude of this observation, it is notable that he also observed oviposition by *Ma. 'rebeli'* on *Gentianella germanica* (Willd.) E.F. Warb. on the same site (Jutzeler 1988). This region is distant and isolated by high mountains from the type locality of *Ma. rebeli*. Genetic studies and more knowledge about the host ant specificity of this Swiss population would be necessary to decide whether it is really *Ma. rebeli* (and e.g. not *Ma.alcon X*) and if its main host ant is really *My. sulcinodis*. Here it should be noted that specimens, phenotypically completely identical with the type specimens of *Ma. rebeli*, have also been collected from some high mountain habitats of Switzerland (Pontresina, 21. 07. 1907, leg. F.W. Dadd, coll. Zoological State Collection, Munich, checked by ZV).

Our results for *Ma.alcon X*, showing *My. sabuleti* as host, are in agreement with previous studies (e.g. Meyer-Hozak 2000, Tartally et al. 2008) that *My. sabuleti* is one of the most important host ants of this butterfly, and which has been already identified as the main host in other Austrian sites by Steiner et al. (2003).

The presence of *I. cf. eumerus* in *Maculinea* pupae appears to be a good indication that a given ant species is a suitable host ant of *Maculinea* butterflies (Thomas et al. 2002), so the relatively high infestation rate by the parasitoid is consistent with *My. sabuleti* being a suitable host of *Ma.alcon X*, and with *My. sulcinodis* being a suitable host of *Ma. rebeli* in the sites studied here.

The one empty *Myrmica* nest found to be infested with *Ma.alcon X* confirms that colonies of various *Myrmica* species can migrate (Radchenko and Elmes 2010). Therefore it could potentially happen that a host *Myrmica* colony moves out and leaves the *Maculinea* pupae in the nest and another *Myrmica* species occupies the empty nest, complete with *Maculinea* pupae, leading to an erroneously recorded 'secondary host ant' (Thomas et al. 2005).

It is almost certain that *Manica rubida* Latreille, 1802 is not available as a potential host for the populations studied here, despite the presence of this ant in this region. *Manica rubida* is closely related genetically (Jansen and Savolainen 2010), and similar chemically (Errard et al. 2006), to *Myrmica* spp. and shows potential suitability as a host of the *Ma.alcon* group in the laboratory (Tartally 2004). This ant is common in the nearby sites of both butterflies, typically in the border of spruce forests, but was not found in

the patches with *Gentiana cruciata* or *Gentianella rhaetica*. It also should be noted that despite the common presence of other gentian species (e.g. *Gentiana asclepiadea* L., see also: Kudrna and Fric 2013) in this region, *Maculinea* eggs were never observed on them.

The unusual host ant use of *Ma. rebeli* in the Alpine sites could be constrained by the distinctive composition of the *Myrmica* community found there. Although *Maculinea* populations can adapt to locally available *Myrmica* species (e.g. Nash et al. 2008, Tartally 2005, Tartally et al. 2013), the unique combination of host ant and host plant usage of these *Ma. rebeli* populations means that the nominotypic *Ma. rebeli* should be treated as a distinct Conservationally Significant Unit (see Maes et al. 2004), separated biologically and ecologically from both *Ma.alcon X* and *Ma.alcon H*. Further studies on the host ant and host plant specificity of *Ma. rebeli* and genetic comparison of these butterflies is necessary to qualify the degree of ecological and genetic relationships within the *Ma.alcon* group, and also to draw well-supported taxonomical conclusions on the status of the nominotypical *Maculinea rebeli* versus *Ma. rebeli* auct. (*Ma.alcon X*).

## Conclusion

It should be concluded that *Ma. rebeli* does not simply represent an individual form of *Ma.alcon* (as considered by Kudrna and Fric 2013) but it should be considered as at least an ecological form adapted to high mountain conditions both in its initial food plant and host ant species. In addition, it should be emphasized that *Ma.alcon X* (= *Ma. rebeli* auct. nec Hirschke) cannot be synonymised with *Ma. rebeli* (Hirschke, 1904).

## Acknowledgements

We dedicate this manuscript to the memory of our co-author and friend Anton Koschuh (Fig. 10) who unfortunately could not see the final version of this paper. This survey could not have been carried out without his initiation, enthusiasm and deep knowledge of the habitats. This publication is also dedicated to the memory of Prof. Klaus Horstmann, who provided invaluable assistance in confirming our determinations of *Ichneumon eumerus* in previous studies (e.g. Tartally 2008, Tartally et al. 2013) but sadly passed away before he could be involved in this current work.

We are grateful for the help on the manuscript for David R. Nash, Enikő Tóth, Gábor Sramkó and two anonymous referees.

AT was supported by a Marie Curie Career Integration Grant within the 7th European Community Framework Programme, by the TÁMOP-4.2.2/B-10/1-2010-0024 project (the project is co-financed by the European Union and the European Social Fund) and by a 'Bolyai János' scholarship of the Hungarian Academy of Sciences (MTA). AK was supported by the permission of the Nature Conservation Authority of Styria. ZV was supported by the Hungarian National Science Foundation (OTKA 84071).



**Figure 10.** Anton Koschuh on his way to Zeiritz (23.06.2012) (photo: AT).

## References

- Akino T, Knapp JJ, Thomas JA, Elmes GW (1999) Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings of the Royal Society of London, Series B* 266: 1419–1426. doi: 10.1098/rspb.1999.0796
- Als TD, Nash DR, Boomsma JJ (2002) Geographical variation in host-ant specificity of the parasitic butterfly *Maculinea alcon* in Denmark. *Ecological Entomology* 27: 403–414. doi: 10.1046/j.1365-2311.2002.00427.x
- Als TD, Vila R, Kandul NP, Nash DR, Yen S-H, Hsu Y-F, Mignault AA, Boomsma JJ, Pierce NE (2004) The evolution of alternative parasitic life histories in large blue butterflies. *Nature* 432: 386–390. doi: 10.1038/nature03020
- Balletto E, Bonelli S, Settele J, Thomas JA, Verovnik R, Wahlberg N (2010) Case 3508 *Maculinea* Van Eecke, 1915 (Lepidoptera: Lycaenidae): proposed precedence over *Phengaris* Doherty, 1891. *The Bulletin of zoological nomenclature* 67: 129–132. <http://iczn.org/content/case-3508-maculinea-van-eecke-1915-lepidoptera-lycaenidae-proposed-precedence-over-phengaris>
- Barbero F, Thomas JA, Bonelli S, Balletto E, Schönrogge K (2009) Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science* 323: 782–5. doi: 10.1126/science.1163583
- Berezcki J, Pecsénye K, Peregovits L, Varga Z (2005) Pattern of genetic differentiation in the *Maculinea alcon* species group (Lepidoptera, Lycaenidae) in Central Europe. *Journal of Zoological Systematics and Evolutionary Research* 43: 157–165. doi: 10.1111/j.1439-0469.2005.00305.x

- Czechowski W, Radchenko A, Czechowska W, Vepsäläinen K (2012) The ants of Poland with reference to the myrmecofauna of Europe - Fauna Poloniae Vol. 4 New series. Museum and Institute of Zoology of the Polish Academy of Sciences and Natura optima dux Foundation, Warszawa, 496 pp.
- Elmes GW, Thomas JA, Hammarstedt O, Munguira ML, Martin J, van der Made JG (1994) Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly, *Maculinea alcon* (Denis et Schff.) (Lepidoptera). *Memorabilia Zoologica* 48: 55–68.
- Elmes GW, Thomas JA, Wardlaw JC, Hochberg ME, Clarke RT, Simcox DJ (1998) The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. *Journal of Insect Conservation* 2: 67–68. doi: 10.1023/A:1009696823965
- Errard C, Hefetz A, Jaisson P (2006) Social discrimination tuning in ants: template formation and chemical similarity. *Behavioral Ecology and Sociobiology* 59: 353–363. doi: 10.1007/s00265-005-0058-z
- Fric Z, Wahlberg N, Pech P, Zrzavý J (2007) Phylogeny and classification of the *Phengaris-Maculinea* clade (Lepidoptera: Lycaenidae): total evidence and phylogenetic species concepts. *Systematic Entomology* 32: 558–567. doi: 10.1111/j.1365-3113.2007.00387.x
- Glaser F (2006) Biogeography, diversity, and vertical distribution of ants (Hymenoptera: Formicidae) in Vorarlberg, Austria. *Myrmecological News* 8: 263–270. [http://myrmecologicalnews.org/cms/images/pdf/volume8/mn8\\_263-270\\_non-printable.pdf](http://myrmecologicalnews.org/cms/images/pdf/volume8/mn8_263-270_non-printable.pdf)
- Greimler J, Park J-M, Schneeweiss H (2011) *Gentianella* (Gentianaceae): A model taxon for evolution in the Alps. *Taxon* 60: 427–435. <http://www.ingentaconnect.com/content/iapt/tax/2011/00000060/00000002/art00012>
- Habeler H (2008) Die subalpin-alpinen Lebensräume des Bläulings *Maculinea rebeli* (Hirschke, 1904) in den Ostalpen (Lepidoptera, Lycaenidae). *Joannea Zoologie* 10: 143–164. [http://www.landesmuseum.at/pdf\\_frei\\_remote/JoanZoo\\_10\\_0143-0164.pdf](http://www.landesmuseum.at/pdf_frei_remote/JoanZoo_10_0143-0164.pdf)
- Hirschke H (1905) Eine neue hochalpine Form der *Lycaena Alcon* F. aus den steirischen Alpen. *Jahres-Bericht des Wiener Entomol Vereines* 15: 1–3.
- Höttinger H, Schlick-Steiner BC, Steiner FM (2003) The Alcon blue *Maculinea alcon* (Lepidoptera: Lycaenidae) in eastern Austria: status and conservation measures. *Ekologia (Bratislava)* 22: 107–118.
- ICZN (2012) Official Lists and Indexes of Names in Zoology, Updated March 2012. <http://iczn.org/sites/iczn.org/files/officialists.pdf> [Accessed: 08 April 2014]
- Jansen G, Savolainen R (2010) Molecular phylogeny of the ant tribe Myrmicini (Hymenoptera: Formicidae). *Zoological Journal of the Linnean Society* 160: 482–495. doi: 10.1111/j.1096-3642.2009.00604.x
- Jutzeler D (1988) Fund von *Maculinea rebeli* (Hirschke, 1904) im Glarnerland (Lepidoptera, Lycaenidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 38: 124–125.
- Jutzeler D (1989) *Maculinea rebeli* (Hirschke) Ein Raupenfund im Glarnerland (Lepidoptera: Lycaenidae). *Mitteilungen der Entomologischen Gesellschaft Basel* 39: 92–93.
- Kolev Z (2002) The species of *Maculinea* van Eecke, 1915 in Bulgaria: distribution, state of knowledge and conservation status (Lycaenidae). *Nota Lepidopterologica* 25: 177–190.

- Kudrna O, Fric ZF (2013) On the identity and taxonomic status of *Lycaena alcon rebeli* Hirschke, 1905 — a long story of confusion and ignorance resulting in the fabrication of a “ghost species” (Lepidoptera: Lycaenidae). *Nachrichten des Entomologischen Vereins Apollo* 34: 117–124.
- Maes D, Vanreusel W, Talloen W, Dyck H Van (2004) Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). *Biological Conservation* 120: 229–241. doi: 10.1016/j.biocon.2004.02.018
- Meyer-Hozak C (2000) Population Biology of *Maculinea rebeli* (Lepidoptera: Lycaenidae) on the Chalk Grasslands of Eastern Westphalia (Germany) and Implications for Conservation. *Journal of Insect Conservation* 4: 63–72. doi: 10.1023/A:1009695031802
- Munguira ML, Martín J (Eds) (1999) Action plan for the *Maculinea* butterflies in Europe. *Nature and Environment*, No. 97. Council of Europe Publishing, Strasbourg, 64 pp.
- Nash DR (2014) MacSamp. <http://www.zi.ku.dk/personal/drnash/download/MacSamp.html> [Accessed: 08 April 2014]
- Nash DR, Als TD, Maile R, Jones GR, Boomsma JJ (2008) A mosaic of chemical coevolution in a large blue butterfly. *Science* 319: 88–90. doi: 10.1126/science.1149180
- Pech P, Fric Z, Konvička M (2007) Species-specificity of the *Phengaris (Maculinea)-Myrmica* host system: fact or myth? (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae). *Sociobiology* 50: 983–1003. [http://users.prf.jcu.cz/aescu/pech\\_2007\\_sociobiology.pdf](http://users.prf.jcu.cz/aescu/pech_2007_sociobiology.pdf)
- Pecsénye K, Bereczki J, Tihanyi B, Tóth A, Peregovits L, Varga Z (2007) Genetic differentiation among the *Maculinea* species (Lepidoptera: Lycaenidae) in eastern Central Europe. *Biological Journal of the Linnean Society* 91: 11–21. doi: 10.1111/j.1095-8312.2007.00781.x
- Radchenko AG, Elmes GW (2010) *Myrmica* (Hymenoptera: Formicidae) ants of the Old World. *Fauna Mundi* 3: 1–789.
- Savela M (2014) Lepidoptera and some other life forms. [http://ftp.funet.fi/index/Tree\\_of\\_life/insecta/lepidoptera/ditrysia/papilionoidea/lycaenidae/polyommata/maculinea/index.html](http://ftp.funet.fi/index/Tree_of_life/insecta/lepidoptera/ditrysia/papilionoidea/lycaenidae/polyommata/maculinea/index.html) [Accessed 08 April 2014]
- Schönrogge K, Wardlaw JC, Thomas JA, Elmes GW (2000) Polymorphic growth rates in myrmecophilous insects. *Proceedings of the Royal Society of London, Series B* 267: 771–777. doi: 10.1098/rspb.2000.1070
- Seifert B (1988) A taxonomic revision of the *Myrmica* species of Europe, Asia Minor, and Caucasus (Hymenoptera, Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 62: 1–75.
- Settele J, Kühn E (2009) Insect conservation. *Science* 325: 41–42. doi: 10.1126/science.1176892
- Settele J, Kühn E, Thomas JA (Eds) (2005) Studies on the ecology and conservation of butterflies in Europe: species ecology along a European gradient: *Maculinea* butterflies as a model, vol 2. Pensoft Publishers, Sofia-Moscow, 289 pp.
- Sielezniew M, Rutkowski R, Ponikwicka-Tyszko D, Ratkiewicz M, Dziekańska I, Švitra G (2012) Differences in genetic variability between two ecotypes of the endangered myrmecophilous butterfly *Phengaris (=Maculinea) alcon*- the setting of conservation priorities. *Insect Conservation and Diversity* 5: 223–236. doi: 10.1111/j.1752-4598.2011.00163.x
- Sielezniew M, Stankiewicz AM (2004) Simultaneous exploitation of *Myrmica vandeli* and *M. scabrinodis* (Hymenoptera: Formicidae) colonies by the endangered myrmecophilous

- butterfly *Maculinea alcon* (Lepidoptera: Lycaenidae). European Journal of Entomology 101: 693–696. doi: 10.14411/eje.2004.091
- Stankiewicz A, Sielezniew M, Švitra G (2005) *Myrmica schencki* (Hymenoptera: Formicidae) rears *Maculinea rebeli* (Lepidoptera: Lycaenidae) in Lithuania: new evidence for geographical variation of host-ant specificity of an endangered butterfly. Myrmecologische Nachrichten 7: 51–54. [http://myrmecologicalnews.org/cms/images/pdf/volume7/mn7\\_51-54\\_non-printable.pdf](http://myrmecologicalnews.org/cms/images/pdf/volume7/mn7_51-54_non-printable.pdf)
- Steiner FM, Sielezniew M, Schlick-Steiner BC, Höttinger A, Stankiewicz H, Górnicki A (2003) Host specificity revisited: New data on *Myrmica* host ants of the lycaenid butterfly *Maculinea rebeli*. Journal of Insect Conservation 7: 1–6. doi: 10.1023/A:1024763305517
- Tartally A (2004) Is *Manica rubida* (Hymenoptera: Formicidae) a potential host of the *Maculinea alcon* (Lepidoptera: Lycaenidae) group? Myrmecologische Nachrichten 16: 23–27. [http://myrmecologicalnews.org/cms/images/pdf/volume6/mn6\\_23-27\\_printable.pdf](http://myrmecologicalnews.org/cms/images/pdf/volume6/mn6_23-27_printable.pdf)
- Tartally A (2008) Myrmecophily of *Maculinea* butterflies in the Carpathian Basin (Lepidoptera: Lycaenidae). PhD Thesis, University of Debrecen, Debrecen, Hungary, 97 pp. <http://gany-medes.lib.unideb.hu:8080/dea/bitstream/2437/78921/5/ertekezes.pdf> [Accessed: 08 April 2014]
- Tartally A (2005) *Myrmica salina* (Hymenoptera: Formicidae) as a host of *Maculinea alcon* (Lepidoptera: Lycaenidae). Sociobiology 46: 39–43. [http://www.researchgate.net/publication/229424075\\_Myrmica\\_salina\\_\(Hymenoptera\\_Formicidae\)\\_as\\_a\\_host\\_of\\_Maculinea\\_alcon\\_\(Lepidoptera\\_Lycaenidae\)/file/d912f5009b1e41ac61.pdf](http://www.researchgate.net/publication/229424075_Myrmica_salina_(Hymenoptera_Formicidae)_as_a_host_of_Maculinea_alcon_(Lepidoptera_Lycaenidae)/file/d912f5009b1e41ac61.pdf)
- Tartally A, Nash DR, Lengyel S, Varga Z (2008) Patterns of host ant use by sympatric populations of *Maculinea alcon* and *M. “rebeli”* in the Carpathian Basin. Insectes Sociaux 55: 370–381. doi: 10.1007/s00040-008-1015-4
- Tartally A, Rodrigues MC, Brakels P, Arnaldo PS (2013) *Myrmica aloba* (Hymenoptera: Formicidae) hosts isolated populations of a hoverfly, a butterfly and an ichneumon species in NE-Portugal. Journal of Insect Conservation 17: 851–855. doi: 10.1007/s10841-013-9575-7
- Thomas JA, Elmes GW (1998) Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. Ecological Entomology 23: 457–464. doi: 10.1046/j.1365-2311.1998.00153.x
- Thomas JA, Elmes GW, Schönrogge K, Simcox DJ, Settele J (2005) Primary hosts, secondary hosts and ‘non-hosts’: common confusions in the interpretation of host specificity in *Maculinea* butterflies and other social parasites of ants. In: Settele J, Kühn E, Thomas JA (Eds) Studies on the Ecology and Conservation of Butterflies in Europe Vol. 2: Species Ecology along a European Gradient: *Maculinea* Butterflies as a Model. Pensoft Publisher, Sofia-Moscow, 99–104.
- Thomas JA, Elmes GW, Wardlaw JC, Woyciechowski M (1989) Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. Oecologia 79: 452–457. doi: 10.1007/BF00378660
- Thomas JA, Knapp JJ, Akino T, Gerty S, Wakamura S, Simcox DJ, Wardlaw JC, Elmes GW (2002) Parasitoid secretions provoke ant warfare. Nature 417: 505–6. doi: 10.1038/417505a
- Thomas JA, Settele J (2004) Evolutionary biology: butterfly mimics of ants. Nature 432: 283–284. doi: 10.1038/432283a

- Tuzov VK (2000) Guide to the Butterflies of Russia and Adjacent Territories: Libytheidae, Danaidae, Nymphalidae, Riodinidae, Lycaenidae. Vol. 2. Pensoft Publisher, Sofia-Moscow.
- Ugelvig L V, Vila R, Pierce NE, Nash DR (2011) A phylogenetic revision of the *Glaucopsyche* section (Lepidoptera: Lycaenidae), with special focus on the *Phengaris-Maculinea* clade. Molecular Phylogenetics and Evolution 61: 237–43. doi: 10.1016/j.ympev.2011.05.016
- Witek M, Sliwinska EB, Skorka P, Nowicki P, Wantuch M, Vrabec V, Settele J, Woyciechowski M (2008) Host ant specificity of large blue butterflies *Phengaris (Maculinea)* (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe. European Journal of Entomology 108: 871–877. doi: 10.14411/eje.2008.115
- Witek M, Sliwinska EB, Skorka P, Nowicki P, Settele J, Woyciechowski M (2006) Polymorphic growth in larvae of *Maculinea* butterflies, as an example of biennialism in myrmecophilous insects. Oecologia 148: 729–33. doi: 10.1007/s00442-006-0404-5